TRACE FOSSILS ON BADENIAN (MIOCENE) GASTROPODS FROM VÁRPALOTA, HUNGARY

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Abstract

Traces of predation and settlement were studied on gastropods of the Badenian (Middle Miocene) Szabó sand pit at Várpalota. Traces of predation were made by gastropods and malacostracans; settlement traces were produced by sponges, cirriped larvae, annelids and bivalves. The trace-bearing gastropods are inbenthonic or epibenthonic herbivores or carnivores. Number of specimens in each gastropod species, number of damaged shells and quantity of trace fossils are given. An outline of part of the ancient ecological system is provided. The trace fossils provided information on animals without hard skeleton (annelids, poriferans, cirriped larvae, malacostracans). Data have been obtained on the mode of life of certain species, on the feeding habits of naticids and murex, and on their food, species by species. Bioerosion is an important factor in making differences in preservation of fossil faunae.

Introduction

Several authors have studied the Middle Miocene Mollusca fauna of the former Szabó's sand pit at Várpalota. Systematic studies were made by TELEGDI ROTH (1924), SZALAI (1943), WENZ and STRAUSZ (1954) and KECSKEMÉTI–KÖRMENDI (1961).

The fauna is extremely rich in species; besides, many specimens bear damages. Our studies were centered at the latter ones. We examined the several types of trace fossils, and tried to identify the way and the organism which made them. Character and quantity of damages on the representatives of each species was determined; similar studies have not been made before on this material.

The collection of gastropods, which we studied, was made by several collectors in different times, therefore we are not certain, if it represents the composition of the fauna correctly. The studied 75 species are represented by 6200 specimens. Fourtyseven of them bear damages.

The different kinds of holes on the shells were filled by epoxy resin; dissolving the shell by hydrochloric acid the internal mould of the traces could be examined. The forms were enhanced by a thin ammonium chloride film. Traces of boring sponges were studied by X-ray photography to find the siliceous sponge spicules; this method gave negative results.

The whorls of the gastropods were numbered beginning with the last one, as mostly the apex is missing.

Broken lines of the plots represent Poisson standard deviation.

The damages and their agents

Traces of feeding and settlement occur on the studied gastropod shells. Traces of feeding were produced by gastropods and malacostracans, while settlement traces were made by cirriped larvae, annelids, and bivalves.

Damages made by gastropods

Most of the damages are gastropod borings. Considering the mode of life of living gastropods (TATISHVILI et al., 1968; BROMLEY, 1981) the following predators lived at Várpalota: *Terebra*, *Natica*, *Murex*, and *Conus*. *Murex* and *Natica*-type gastropods make borings into the shell of their victim.

a) Naticids

Infaunal mode of life; most of the diet consists of venerid bivalves (TATISHVILI et al., 1968, p. 77; BROMLEY, 1981). Prey gastropods are: *Nassa*, *Aporrhais*, *Turritella*, etc. The boring process consists of a mechanical boring by the proboscis, and a chemical one by solving the carbonate shell by acids. SEM studies helped recognizing the two processes. Cross section of the bored hole is circular forming a semi-globular or crater-like shape (Plate I, figs. 1, 2). Its long axis encloses a variable angle with the surface of the shell (plate I, fig. 3). If the boring was unsuccessful, i. e. the process was stopped, the bottom of the unfinished hole bears a small bulge (plate I, figs. 4 – 6). The predator usually makes the borings through thin areas of the shell; rarely the hole was prepared at the junction of the whorls, where the shell is extremely thick (plate I, fig. 7). Traces of cannibalism can be observed on some species (plate I, fig. 6). Size of the predators is usually 1 to 2,5 cm.

The following species belong to this group: *Natica millepunctata* LAMARCK, *Natica redempta* MICHELOTTI, and *Natica josephinia olla* SERRES.

b) Muricids

Motile, active predators. Epibenthonic forms. Different methods are applied to reach the soft tissues of the victims (TATISHVILI et al., 1968). Valves of some bivalves are forced away, and the tissues are sucked by the proboscis. Peristomes or valve edges of certain bivalve and gastropod species are broken away to reach the animal itself.

The boring is a common result of mechanical and chemical processes.

The muricids feed themselves by epibenthonic forms. The trace of boring is cylindrical, being perpendicular to the surface (ARUA, 1981) (plate I, fig. 8). If the boring process ios unfinished, the incomplete hole bears a smooth surface (plate I, fig. 9). Most of the holes are prepared in areas, where the shell is thin; however, holes along sutures have been observed, too (plate I, fig. 10). Specimens of *Potamides gamlitzensis* HILBER display regenerated borings (plate I, fig. 11).

The following species belong to this group: *Murex rudis syrticus* MAYER, *Hadriania boeckhi* HOERNES, & AUINGER, *Ocinebrina crassilabiata* HILBER, *Murex turonensis pontileviensis* TOURNOUER and *Murex (Tubiconda) spinicostata* BRONN.

Traces of malacostracans

Larger gastropods frequently bear damages made by malacostracans. These are located on the aboral side of the shell, mostly continuing towards the peristome. It is the thinnest part of the shell, containing most of the soft parts of the animal. The opening is 6 to 15 mm in diameter. Its outline is circular, frequently with sharp edges and corners (Fig. 1).

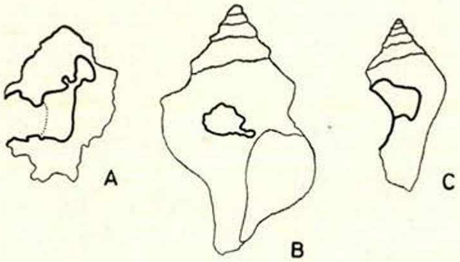


Fig. 1. Traces of malacostracans on gastropod shells.

Traces of sponges

Much less in number than the gastropod borings, pores made by sponges were observed on the genera *Cerithium, Melongena, Potamides, Turritella, Vermetus,* and *Dorsanum*. The traces were produced by the sponge *Cliona* sp. (ARUA, 1981). The pores are observable on the external and internal sides of the shells (Plate I, figs. 12–13).

Two morphological types were recognized up to now (ARUA, 1981; BISHOP, 1975): linear (plate II, fig. 14) or irregular (plate I, figs. 12–13) arrangement of pores with 0.6–1 mm in diameter; or the rare case of spot-like arrangement of very small pores (0.03–0.07 mm). The latter type was not observed in the collection from Várpalota. Frequently the extreme bioerosion of the sponges cause complete damage of the attacked part of the shell (plate II, fig. 15).

Traces of cirripeds

Cirriped larvae belonging to the order Acrothoracica preferred sessile epibenthonic hosts and settled mostly on living animals (Fig. 2).

Two types of traces have been recognized. The first one consists of drop-shaped openings of 1.0–1.8 mm length and 0.15–0.08 mm width.

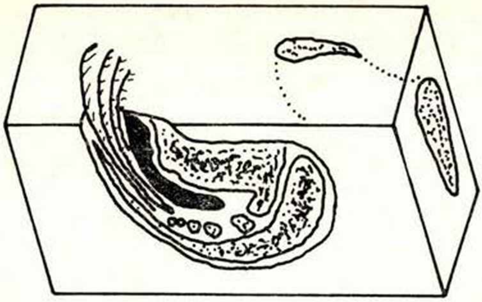


Fig. 2. The cirriped larva in skeletal carbonates (after Seilacher, 1969, fig. 7)

The hole is somewhat larger within the shell. The plastic internal mould shows the form of an apple-seed (plate II, figs. 16 – 18). Part of them lies in irregular arrangement, while others are oriented with their sharp ends towards the aperture of the host. The second type consists of fissure-like depressions forming a linear network, which resembles tiny scratches on the shell. Their length varies between 0.08 and 0.03 mm, while the width is more or less constant (0.01 – 0.03 mm) (ARUA, 1981; SEILACHER, 1969; BISHOP, 1975) (plate II, figs. 19 – 20).

Ultramicroscopic photography revealed traces of etching, proving common activity of mechanical and chemical processes (SEILACHER, 1969).

Traces of cirriped larvae occur on definite parts of the shell: mostly in depressions, like along growth lines, sutures of whorls. They rarely occur on the internal parts of the shell, except in those ones which were inhabited by hermit crabs.

Traces of annelids

Borings of annelids occur only on adult specimens. These are 1 – 3 mm long, 0.5 – 1 mm wide and form two groups. The smaller one is dumb-bell-shaped, not exceeding 1 mm (plate III, fig. 21). The other type is U-shaped (plate III, fig. 22) or irregularly bent (plate III, figs. 23 – 25).

Traces of bivalves

The genera *Vermetus*, *Turritella*, *Hadriania*, *Melongena*, and *Cerithium* bear traces of borers, the valves frequently preserved in the hole. These occur mostly in the thickest parts of the shells (plate IV, figs. 27 – 30). A rare occurrence is shown on Plate IX, fig. 56, displaying a minor *Turritella vermicularis* BROCCHI bored by a relatively large bivalve.

Neither of the above-listed damages have been recognized on the following species (number of specimens shown in brackets): *Tudicla rusticula* BASTEROT (24), *Rissoa (Alvania) curta* DUJARDIN (20), *Calyptraea chinensis* LINNÉ (14), *Pedipes (Nealexia) myotis pisolinus* DESHAYES (14), *Terebra acuminata* BARSAN (11), *Littorina (Littoringosis) scabra alberti*

DUJARDIN (10), *Nassa (Tritia) styriaca* AUINGER (7), *Brotia escheri* BRONGNIART (5), *Pleurotoma badensis* R. HOERNES (5), *Terebra (Subula) fuscata modesta* TRISTAN (5), *Hipponix sulcatus* BORSON (4), *Melanopsis impressa* KRAUSS (4), *Nerita plutonis* BASTEROT (4), *Bittium reticulatum* COSTA (3), *Calyptraea (Bicatillus) deformis* LAMARCK (3), *Clavatula interrupta vitalisi* STRAUSZ (3), *Solarium simplex* BRONN (3), *Crepidula cochlearis* BASTEROT (2), *Dorsanum nodosocostatum ternodosum* HILBER (2), *Ringicula (Ringiculina) auriculata buccinea* BROCCHI (2), *Terebra fuscata plicaria* BASTEROT (2), *Acteon cf. woodi* MAYER (1), *Capulus sulcosus* BROCCHI (1), *Clavatula interrupta* BROCCHI (1), *Conus (Conolithus) dujardini brezinae* HOERNES & AUINGER (1), *Cypraea (Zonaria)* sp. aff. *fabagina* STRAUSZ (1), *Fasciolaria (Pleuroploca) tarbelliana* GRATELOUP (1), *Murex (Muricanthus) turonensis pontileviensis* TOURNOUER (1), *Murex (Tubicauda) spinicostata* BRONN (1), *Potamides (Ptychopotamides) papaveraceus* BASTEROT (1).

The species occurring with more than 10 specimens are discussed below (smaller number of specimens, due to problems of statistics, does not indicate the improbability of traces occurring on them).

Tudicla rusticula BASTEROT

Large size specimens (8 – 10 cm). The very thick shell is ornamented with strong spines. Predators could rardly reach the animal. Almost all specimens were mechanically damaged. Probably the shell was easily damaged after the decay of the animal, thus providing poor substrate for borer settlement.

Rissoa (Alvania) curta DUJARDIN

Usually occurs in large masses on algae or stems of plants. Herbivorous, feeding on lower algae, and diatoms. Very small size (3 – 4 mm only). These are very small pieces of prey for the predators.

Calyptraeans

Phytophagous, feeding on planktonic organisms or detritus feeder. Mode of life: fixed to hard objects, like bivalves or rocks, in the wave agitated zone. It selects a place, where there is low probability of being covered by sediments. Neither the naticids, nor the muricids attack in this zone. Usually this zone is not suitable for the settlement of the other producers of the investigated trace fossils.

Pedipes (Neatexia) myotis pisolina DESHAYES

Smaller than 9 mm. We have no information on its mode of life, therefore we have no idea why it does not bear damages. Possibly it was simply of bad taste for the predators. (Actual observations proved that the predators are selective, do not attack all available species.)

Terebra acuminata Borson

Inbenthonic predator. The shell is extremely elongated, with a very small apical angle. Possibilities include too small size of the soft tissues, hardly accessible soft parts, or that the species itself was dangerous to the attacker.

Littorina scabra alberti Dujardin

Feeding mostly with diatoms and other algae, but is omnivorous. Lives in the fissures of a rocky bottom in the shallow intertidal zone. The shell is small (14 mm), having a thin wall. It escaped attack due to its habitat.

Trace fossil-bearing species

Table I consists numerical data on the occurrence of the discussed types of trace fossils on each species. Detailed description of the species follows the sequence in Table II, displaying species with high damage percentage. The species are ordered according to their mode of life and feeding habits and size.

A) Inbenthos

a) Herbivores

Turritellids

Turritellids feed on diatoms and other algae, filtered from the water adjacent to the bottom. There are several theories on their mode of life (Tatishvili et al., 1968). Most probable is their burrowing in the mud, supported by our observations. Unfinished borings bear the small bulge in their bottoms made by naticids; these holes occur mostly on the 2nd or 3rd coil (Fig. 3). Preys of the naticids are inbenthonic animals; and the borings are located on the coil which is most close to the surface, but contains relatively much food.

Turritella aquitanica Tournouer

It is the 5th species in numbers of our material. Most of the borings are located on the 2nd and 3rd coils (Fig. 3), some of them occurring on the suture between them (plate I, fig. 7). One of the specimens bear trace of pinching by a crab (plate IX. fig. 51).

Turritella (Haustator) eryna partschi Rolle

Three specimens bear gastropod borings on the 2nd and 3rd coils (plate IX, fig. 53). Pores of sponges were observed on 4 specimens.

Turritella turris badensis Sacco

Three specimens bear gastropod borings on the 3rd and 4th coils. Several sponge traces occur. The tiny pores form intersecting lines (plate II, fig. 25). The shell became porous, and broke in after a minor mechanical damage (plate IX, fig. 54).

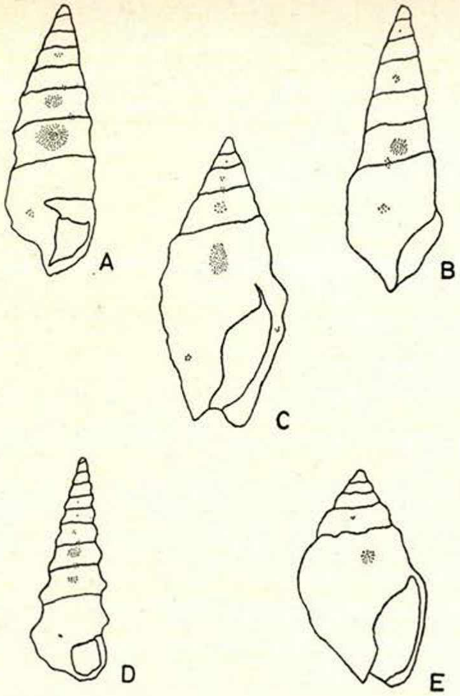


Fig. 3. Position of gastropod borings on the shells.

Turritella vermicularis BROCCHI

The specimen of plate VIII, fig. 55 bears much sponge traces on all sides of the shell, ordered irregularly, Gastropod borings are bowl-shaped, their size suggesting naticids as agents. The damage on plate IX, fig. 56 was made by a boring bivalve; its upper part bears a boring by a naticid. It is supported by the strongly damaged internal part, the missing septa and columella. Probably the boring bivalve chose the empty shell of a gastropod, victim to a naticid. The 2,5 cm long shell – which was not a very stable point on the sea bottom – provided habitat for a relatively large bivalve.

Turritella bicarinata subarchimedes ORBIGNY

The boring is located at the suture between coils 2 and 3 (plate IX, fig. 57).

Protomids

These ones bear borings made by naticids, with circular openings on both the external and internal surfaces. The protomids are related to the genus *Turritella*, therefore these were frequently attacked by naticids preferring inbenthonic animals.

Protoma proto Basterot

There are damages of the 2nd and 3rd coils. The animals attacked range is size from 1.5 to 3 cm: juvenile specimens were among the victims, too.

Protoma proto quadriplicata Basterot

Usually bored on the 3rd coil (plate X, fig. 59).

Species belonging to other groups

Genota ramosa elisae Hoernes & Auinger

It is the seventh species in number of specimens of the collection. Few gastropod boring; no other trace fossils. The boring is bowl-shaped, located above the aperture on coil 2 (plate IX, fig. 58). Its shape indicate a naticid predator, suggesting inbenthonic mode of life for the genus *Genota*. Elongated shape of the shell, the narrow, long aperture and the presence of siphonal canal does not contradict this hypothesis.

Aporrhais pespelecani alatus Eichwald

Feeding on plant detritus and on diatoms and other algae. Burrows into the soft mud up to the apex. The shells are positioned horizontally, with apertures down. The naticid turned the Aporrhais out of the mud and bored it near the aperture (plate X, fig. 60).

b) Carnivores

Nassa dujardini edlaueri Beer

Burrows deep into the mud, appearing to feed only. Predator, but mostly scavenger. Eats fishes, crabs, molluscs.

75% of the damaged specimens were bored on the last coil, part of the traces being located near the inner lip (Fig. 3, plate X, fig. 61). It can be explained by the occurrence of most of the soft parts there. There is a specimen, in which the boring displays bowl-shape, but with smooth bottom (plate X, fig. 62). The latter suggests a naticid as the predator.

Nassa styriaca Auinger

Eleven specimens bear one gastropod boring each, all located on the 2nd coil.

Nassa hungarica Mayer

Plate XI, fig. 63 displays injure regenerated by the animal.

Dorsanum nodosocostatum Hilber

It belongs to the inbenthonic Nassas. It is eaten by molluscs, either living or after the death (Tatishvili et al., 1968). The specimens bear gastropod and sponge traces. There is a regenerated injure on the 2nd coil, on the aboral side (plate XI, fig. 64). There is the conspicuous bulge on the bottom of the unfinished borings, characteristic of the naticids (plate I, fig. 4). Eighty percent of the traces is located on the last coil, above the inner lip (Fig. 3). It also indicated the relationships with the Nassas. Unfinished borings were not completed not due to the thickness of the shell, but the predator might have been disturbed. There are 3 borings on the last coil on one of the specimens. Plate IX, fig. 65 shows a specimen bearing a circular boring with half-globular cross-section. There is the small bulge on the bottom of the unfinished boring. Plate I, fig. 1 shows a circular trace, too, but the hollow is elliptical. Plate IX, fig. 66 displays a biscuit-shaped boring due to the ornamentation of the shell. The locations of the attack on 142 specimens are plotted on Fig. 3.

Terebra basteroti NYST

Predators, burrowing in sandy bottom. One of the 8 specimens bears a gastropod boring on the 4th coil. Form of the hole and mode of life of the gastropod indicate the predators as naticids (Plate XI, fig. 67).

Naticids

Natica redempta MICHELOTTI

A single one of 51 specimens display a boring; the predator might have been a naticid, supplying evidence for cannibalism.

Natica josephinia olla SERRES

Unfinished borings occur on 2 specimens. Bottom of the holes are smooth, indicating *Murex* as predator (plate VII, fig. 42). There is a strong round, bulging thickening in the umbilicus. The predator bored just in the middle of it. So unfortunate selection of the location of the boring is very rare (plate I, fig. 9; plate VII, fig. 43).

Natica millepunctata LANARCK

Six borings were observed; four of them are located on the inner lips of the victim, two of them are on the aboral side. Traces of cannibalism can be observed. A regular, cylindrical boring was prepared, hollowing downwards. There is a tiny bulge in the centre of the bottom of the unfinished boring, indicating the predators as naticids (plate VII, figs. 44–45).

B) Epibenthos

a) Herbivores

Theodoxus picta FÉRUSSAC

Only 3 specimens bear borings among a population of 142. It may be due to the small (5.5 cm) size of the shell. Epibenthonic form, the predator might have been a muricid.

Drillia allionii BELLARDI

Gastropod borings occur on coils 2 and 3. Probably the most sensitive soft part of the animal was located here. Half of the bored specimens bear two completed borings (plate V, fig. 31); either the same predator prepared the two holes, because one was not sufficient to empty the shell of the victim, or two gastropods attacked simultaneously. A third answer to the problem of the double borings may be that the victim escaped after the preparation of the first one, but was catched again.

If the boring process was begun in a thick area, the hole lies obliquely to the surface. Identity of the predator cannot be determined from the traces.

Potamids

Largest number of specimens. Epibenthonic, herbivorous, feeding on algae. Depth range coincides with that of the algae: occur down to 50 m Prefer sandy bottom (TATISHVILI et al. 1968).

Potamides (Pirenella) gamlitzensis HILBER

One gastropod boring occurs on each shells. The borings were rarely prepared on the sutures between the coils. Apparently the boring is oblique to the surface at the sutures and nodes (plate I, fig. 8). Smooth bottom of unfinished borings indicate *Murex* predators. Mode of life of the animals suggests the same.

One specimen bears a regenerated boring (plate I, fig. 11).

Location of the boring is on coils 2 or 3 (plate V, fig. 32). This area might have yielded the largest or best food for the predator (Fig. 3).

Potamides (Pirenella) moravicus HÖRNES

Almost 10% of the specimens bear Murex traces. Most of the borings are on coil 2, like on *P. gamlitzensis* (Fig. 3). There are no unfinished borings. The suture between the coils was bored in 9 cases, forming two openings on the shell. The trace is circular on the surface (plate V, fig. 33).

Two of 80 specimens of *Potamides (Pirenella) pictus* DEFRANCE & BASTEROT, and one of 75 specimens of *Potamides (Pirenella) gamlitzensis* ROLLE were bored by muricids.

Potamides (Terebralia) bidentatus perrugatus HILBER

Large size (6 – 7 cm), thick-shelled forms. One of them bears traces of boring bivalves, located in depressions among the ornaments (plate IV, fig. 30).

Potamides (Terebralia) bidentatus lignitarium EICHWALD

There are sponge-made pores on a well-worn, broken shell.

Potamides (Terebralia) bidentatus margaritifer SACCO

Dumb-bell-shaped worm traces occur on the lower part of the last coil (plate VI, fig. 40). Traces of boring bivalves occur, too (plate IV, figs. 28–29).

Cerithids

Their mode of life is similar to that of the potamids, consequently their attacker was the same.

Cerithium exdoliolum SACCO

There is a gastropod boring between the 2nd and 3rd coils. It is circular on the surface and is cylindrical downwards; its side is perpendicular to the surface (plate I, fig. 10). Plate IV, fig. 27 displays a boring bivalve within the shell. Traces os sponges were observed on plate V, figs. 34–35. The shell is broken between the linear pores.

One of 15 specimens of *Cerithium rubiginosum pseudobliquostoma* SZALAI and two of 12 specimens of *Cerithium vulgatum europaeum* MAYER were bored by muricids.

Species belonging to other groups

Columbella (Alia) helvetica MAYER

Preferred sandy bottom. Worm trace is shown on plate III, fig. 21.

Pusionella pseudofusus palatina STRAUSZ

Three of 18 specimens display trace fossils: two gastropod borings and the third specimen bears traces of cirriped larvae. Both types of the latter one – the apple-seed-like and the scratch-like – are shown on plate V, fig. 36 and plate VI, fig. 37.

Ancilla glandiformis LAMARCK

95 specimens of robust, thick-walled shells (3–4 cm). Several traces occur, except gastropod borings (probably due to the thick wall). There are six specimens with crab pinches. The crabs attacked on the aboral side (Fig. 1, plate VI, fig. 38). If the location is not good, the crab breaks the shell at the outer lip (plate VI, fig. 39). The other damages were formed after the death of the animal. Cirriped larval traces were found on a single specimen only, but both types occurred on the same shell (plate II, figs. 17–20). (A detailed description see under 'Damages and their agents'.) The larger, drop-shaped traces occur on the columella only, while the smaller, scratch-like traces cover almost the whole surface, even the inner sides (habitat of a hermit crab). Sponge pores occur, too. One of the shells served as bottom for a boring bivalve. It bored itself into the apex. The open-

ing is 2 mm long, 1.5 mm wide, ellipsoidal in shape. There is a worm trace above the aperture of one of the specimens. The U-shaped 'tunnels' and other traces are not more than 6 mm long, and occur above the aperture. The worm has settled after the death of the gastropod, since the aperture must have turned upwards to provide a good substratum.

Vermetus arenarius LINNÉ

Epibenthonic, phytophagous forms. There are minor bivalves bored into the thick shells; also sponge pores occur (plate I, figs. 12–13).

Melongena cornuta AGASSIZ

Largest specimens at Várpalota, with the thickest shell (up to 15 cm). It was embedded in the sandy bottom due to its considerable weight. Therefore one side is intact, while the other served as substratum for several sessile organisms. All the traces were formed after the death of the animal. Most of the boring organisms are bivalves (plate VII, fig. 41), and worms. Plate II, fig. 14 displays pore lines of sponges.

b) Predators

Muricids

Ocinebrina crassilabiata HILBER

There are several crab pinches on the shells, located aborally. It was the most easily available part of the animal with the thinner shell than around the aperture. The damage is always on the last coil, because most of the soft parts occur here (plate VIII, fig. 46).

Hadriania boeckhi (Tritonalia sublavata) HOERNES & AUINGER

There is a pinch of crab on plate VIII, fig. 47. There are worm traces above the crab pinches. Another gastropod bears a boring bivalve within the thickened peristome (plate IV, fig. 26).

Murex rudis syrticus MAYER

There was a single, highly bored specimen. The animal might have been killed by a crab (plate VIII, fig. 49). The trace of the pinch can be well observed; after the initial pinch the predator broke the shell all along to the aperture. After death the shell was inhabited by bivalves (plate VIII, fig. 50).

Eutriofusus burdigalensis DEFRANCE

Three of 37 specimens were bored by gastropods, all of them are juvenile ones. One of them bear a crab pinch (plate VIII, rig. 48).

Conclusions

The trace fossils of the Várpalota fauna have preseved information on the non-fossilizable elements of the community: worms, sponges, cirriped larvae. Besides data have been obtained on the mode of life and habitat of certain species (e. g. *Genota ramosa elisae*) .Information was collected on the special feeding habits of some gastropods: the boring. The location of the best point to bore might have been selected according to vulnerability of the soft parts (position of the visceral sack), availability, thickness of shell, location of the most digestable soft tissue. Most of the borings are located on certain areas of the shell (Fig. 3). The position of borings is the same on similar shells (Fig. 3). Besides this general rule, several ill-located borings have been observed (e. g. at the suture between two coils).

Unfinished borings indicate that the victim had escaped. It may be one of the reasons that in some cases there are two, even three borings on the shell. The victim had escaped, but another predator have attacked it, killing it finally. We can wonder, why it did not use the existing boring. Successful escapes are indicated by regenerated borings. The double borings may have been made by two predators simultaneously, or by a single one, which needed two holes to fully extract the soft tissues. In the previous case the quantity of food was not enough to cover the energy needs of boring.

Table II – containing the important damaged species – shows that herbivorous gastropods dominate the population, in number of species and specimens as well, corresponding to the composition of the natural food chain.

Some palaeoecological conclusions have been drawn. Altogether 8 boring gastropod species lived in the Badenian sea of Várpalota, represented by 385 specimens. These have bored 30 herbivorous species, represented by 650 specimens. Figures 4 and 5 show the species distribution of the victims of muricids and naticids. Looking both the specimen number and the percentage we can observe that the species with most members were most

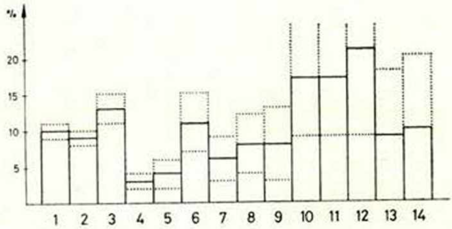


Fig. 4. Percentage of bored specimens of the species attacked by naticids (the species represented by more than 10 individuals are listed only). 1. *Dorsanum nodosocostatum* 2. *Nassa dujardini edlaueri* 3. *Turritella aquitanica* 4. *Genota ramosa elisae* 5. *Rimella (Dientmochilus) decussata* 6. *Drillia allionii* 7. *Turritella partschi* 8. *Protoma proto* 9. *Turritella turris badensis* 10. *Nassa hungarica* 11. *Protoma inaequiplicata* 12. *Turritella vermicularis* 13. *Nassa styriaca* 14. *Aporrhais pespelecani alatus*

Table I.

Number of damaged specimens of each species and their trace fossils

Species	Gastropod	Sponge	Worm	Crab	Cirriped	Bivalve	Number of specimens
Potamides (Pirenella) gamlitzensis	257	0	0	0	0	0	1669
Dorsanum nodosocostatum	142	2	0	0	0	0	1493
Potamides (Pirenella) moravicus	92	0	0	0	0	0	951
Nassa dujardini edlaueri	48	0	0	0	0	0	521
Turritella aquitanica	59	4	1	1	0	0	444
Natica millepunctata	6	0	0	0	0	0	215
Genota ramosa elisae	4	0	0	0	0	0	149
Theodoxus picta	4	0	0	0	0	0	142
Ancilla glandiformis	0	0	0	6	1	0	95
Potamides (Pirenella) pictus	2	0	0	0	0	0	80
Rimella (Dientmochilus) decussata	2	0	0	0	0	0	78
Potamides gamlitzensis theodiscus	1	0	0	0	0	0	75
Drillia allionii	8	0	0	0	0	0	71
Turritella partschi	3	4	0	0	0	0	52
Natica redempta	1	0	0	1	0	0	51
Protoma proto	3	0	0	1	0	0	39
Natica josephinia olla	3	0	0	0	0	0	38
Turritella turris badensis	3	3	1	0	0	3	37
Potamides bidentatus margaritifer	0	0	1	0	0	3	37
Euthriofusus burdigalensis	3	0	0	1	0	0	32
Potamides bidentatus lignitarum	0	1	0	0	1	0	36
Hadriania boeckhi-Tritonalia sublavata	0	0	1	2	0	1	32
Potamides bidentatus perrugatus	0	0	0	0	0	1	31
Nassa hungarica	4	0	0	0	0	0	24
Vermetus arenarius	0	1	0	0	0	1	20
Protoma inaequiplicata	4	0	0	0	0	0	24
Pusionella pseudofusus palatina	2	0	0	0	1	0	18
Cerithium rubiginosum pseudobliquistoma	1	0	0	0	0	0	15
Cerithium exdoliolum	2	1	0	1	0	0	15
Turritella vermicularis	3	0	0	0	0	0	14
Brotia escheri inornata	1	0	0	0	0	0	13
Columbella (Alia) helvetica	0	0	0	2	0	0	12
Cerithium vulgatum europaeum	2	0	0	0	0	0	12
Nassa styriaca	1	0	0	0	0	0	11
Ocinebrina (Tritonalia) crassilabiata	0	0	0	3	0	0	10
Aporrhais pespelecani alatus	1	0	0	0	0	0	10
Turritella bicarinata subarchimedes	1	0	0	0	0	0	9
Columbella fallax	1	0	0	0	0	0	9
Melongena cornuta	0	3	1	0	0	0	8
Terebra basteroti	1	0	0	0	0	0	8
Columbella moravica	1	0	0	0	1	0	7
Gibbula buchi	1	0	0	0	0	0	6
Gibbula biangulata	1	0	0	0	0	0	4
Solarium semiquamosum bisulcatum	2	0	0	0	0	0	2
Murex rudis syrticus	0	0	0	1	0	1	1

Table II.

Damaged species and their damages, grouped according to their mode of life, and their size within each group.

(N = naticids, M = muricids).

		SPECIES	Gastr. N	Gastr. M	Crab	Sponge	Cirriped	Bivalve	Worm	Number of specimens
INBENTHONIC	HERBIVORE	*Turritella aquitanica*	59		1	4		1		444
		Turritella eryna partschi	3			4				52
		Turritella turris badensis	3			3		1	3	37
		Turritella vermicularis	3							14
		Turritella bicarinata subarchimedes	1							9
		Genota ramosa elisae	4							149
		Protoma proto	3		1					39
		Protoma inaequiplicata	4							24
		Aporrhais pespelecani alatus	1							10
	CARNIVORE	*Nassa dujardini edlaueri*	48							521
		Dorsanum nodosocostatum	142			2				1493
		Terebra basteroti	1							8
		Nassa styriaca	1							11
		Nassa hungarica	4							24
		Natica redempta		1	1					51
		Natica josephinia olla	1	2						38
		Natica millepunctata	2	4						215
EPIBENTHONIC	HERBIVORE	*Theodoxus picta*		4						142
		Drillia allionii		8						71
		Potamides (Pirenella) gamlitzensis		257						1669
		Potamides (Pirenella) moravicus		92						951
		Potamides (Pirenella) pictus		2						80
		Potamides gamlitzensis theodiscus		1						75
		Cerithium exdoliolum		2	1	1				15
		Columbella (Alia) helvetica			2					12
		Pusionella pseudofusus palatina		2			1			18
		Ancilla glandiformis			6		1			95
		Vermetus arenarius				1			1	20
		Potamides bidentatus perrugatus							1	31
		Potamides bidentatus lignitarum				1	1			36
		Potamides bidentatus margaritifer						1	3	37
		Melongena cornuta				3		1		8
	CARN.	*Ocinebrina (Tritonalia) crassilabiata*			3				1	10
		Hadriania boeckhi-Tritonalia sublavata			2			1	1	32
		Euthriofusus burdigalensis		3	1					32
		Murex rudis syrticus			1				1	1

Pl. I

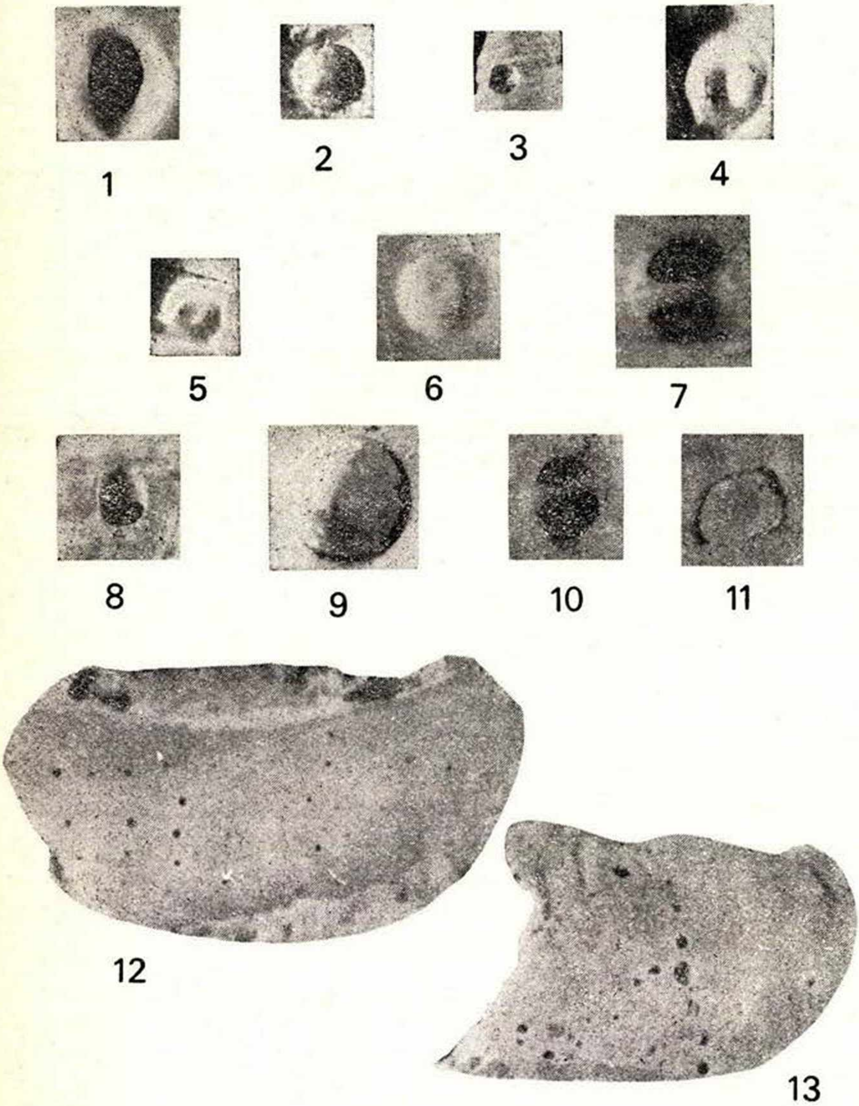
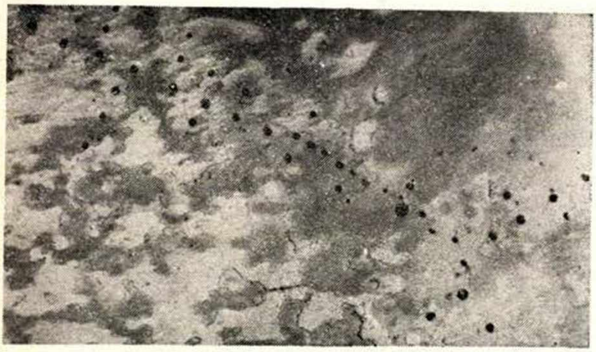


PLATE I.

1. Naticid boring on the gastropod *Dorsanum nodosocostatum* (7,5x)
2. Naticid boring on the gastropod *Nassa dujardini edlaueri* (6x)
3. Naticid boring on the gastropod *Turritella vermicularis* (1.5x)
4. Naticid boring on the gastropod *Dorsanum nodosocostatum.* (7.2x)
5. Naticid boring on the gastropod *Turritella vermicularis* (4x)
6. Naticid boring on the gastropod *Natica millepunctata* (5x)
7. Naticid boring on the gastropod *Turritella aquitanica* (5x)
8. Muricid boring on the gastropod *Pirenella gamlitzensis* (2.4x)
9. Muricid boring on the gastropod *Natica josephinia olla* (2.2x)
10. Muricid boring on the gastropod *Cerithium exdoliolum* (1.8)
11. Muricid boring on the gastropod *Pirenella gamlitzensis* (3x)
12. Sponge pores on the gastropod *Vermetus arenorius* internal surface (4.5x)
13. Sponge pores on the gastropod *Vermetus arenorius* external surface.

Pl. II



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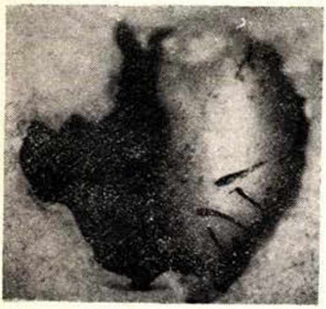

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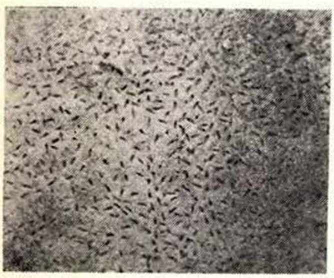

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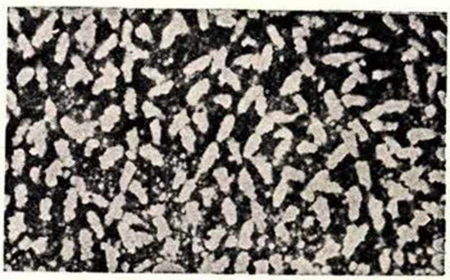

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PLATE II.

14. Sponge pores on the columella of *Melongena (Galeodes) cornuta* (3.2x)
15. Broken pores of sponges in *Turritella turris* (2.5x)
16. Cirriped larval traces on the columella of *Ancilla glandiformis* (3.2x)
17. Plastic internal mould of the shell fragment on Fig. 16. (8x)
18. Cirriped larval traces on the shell of *Tritonalia sublavata* (3.5)
19. Cirriped larval traces on the spire of *Ancilla glandiformis* (5x)
20. Plastic internal moulds of the shell fragment on Fig. 19. (10x)

Pl. III

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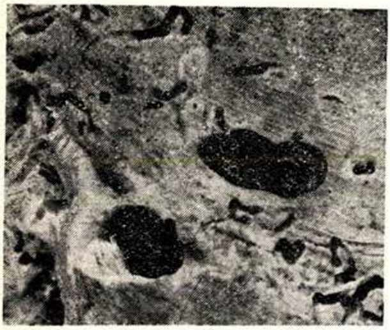

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PLATE III.

21. Dumb-bell-shaped worm traces on the spire of the gastropod *Columbella (Alia) helvetica* Mayer (2x)
22. Plastic internal mould of U-shaped worm traces (4x)
23. Sites of worm tracks and boring bivalves on the spire of *Melongena cornuta* (2.5)
24. Sites of worm tracks and boring bivalves on the spire of worm tracks and boring bivalves (2.5x)
25. Plastic internal mould of worm tracks and boring bivalves on the spire of *Melongena cornuta* (2.5x)

PI. IV

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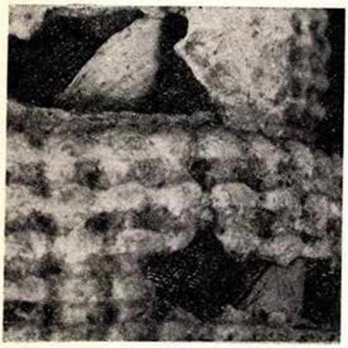

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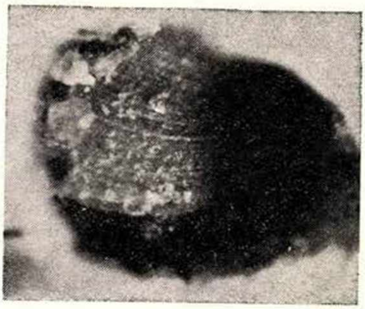

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PLATE IV.

26. Boring bivalve on the outer lip of *Hadriania boeckhi* (6x)
27. A boring bivalve located in the shell of *Cerithium exdoliolum* (9.5x)
28. Boring bivalve in the shell of *Potamides bidentatus* (4x)
29. Boring bivalve in the shell of *Potamides bidentatus* (4x)
30. Boring bivalve among the nodes of the shell of *Potamides bidentatus* (40x)

Pl. V

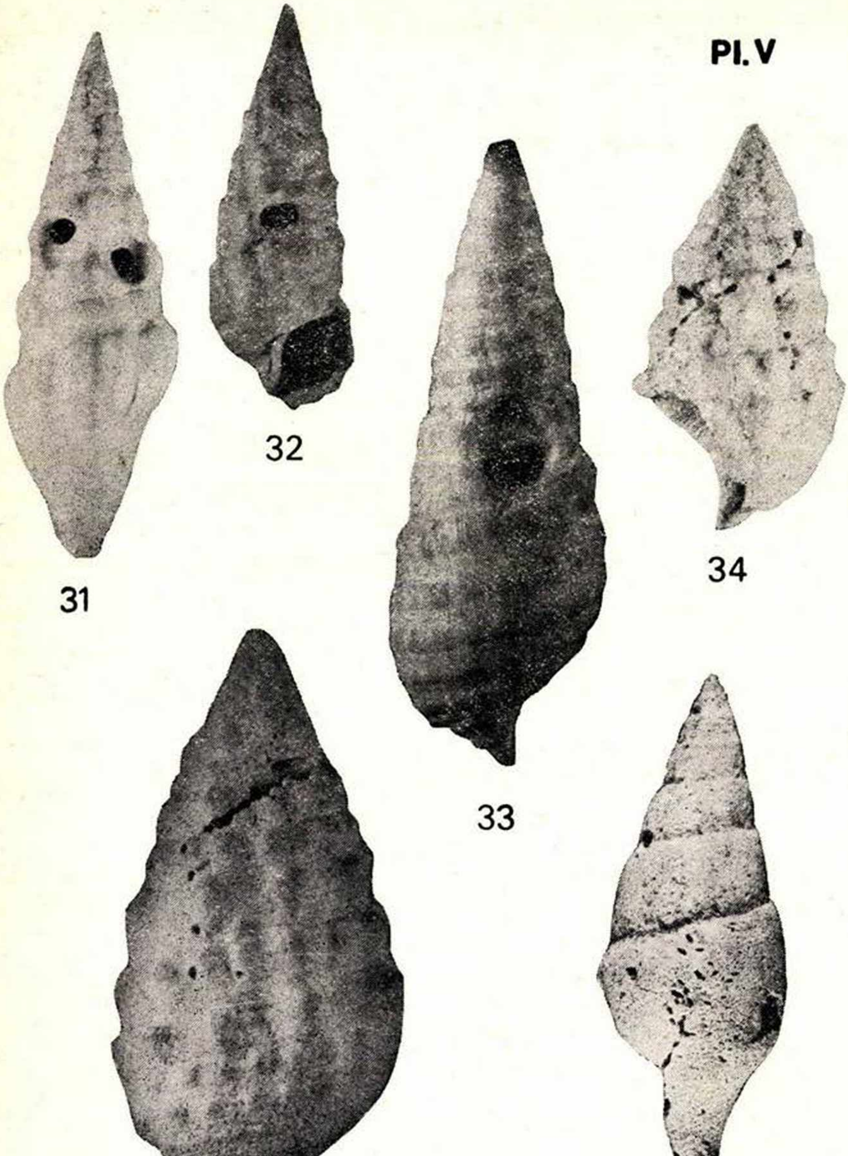
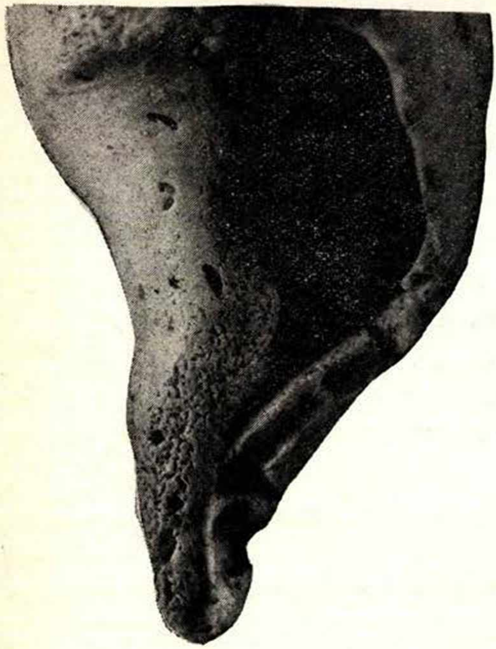


PLATE V.

31. *Drillia allionii* with two muricid borings (3.8)
32. *Pirenella gamlitzensis* with muricid boring (2.5)
33. *Pirenella moravicus* with muricid boring (3.8x)
34. *Cerithium exdoliolum* with sponge pores (3.5x)
35. *Cerithium exdoliolum* with sponge pores and their breaks (4.8)

Pl. VI



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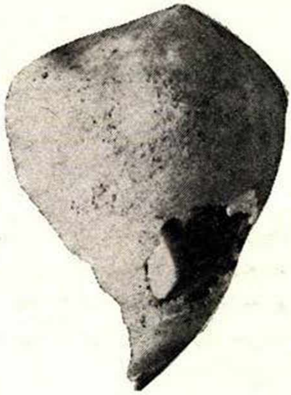

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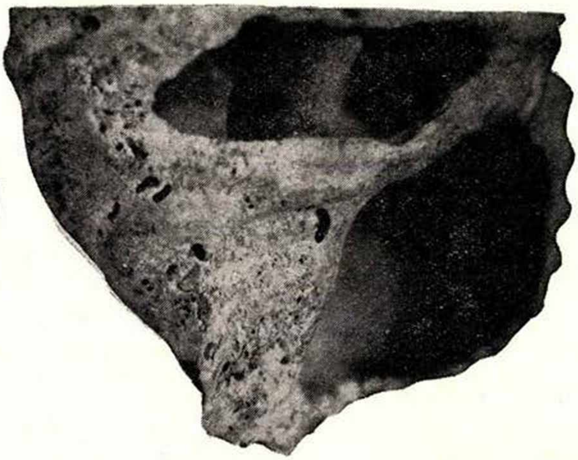

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PLATE VI.

37. *Pusionella pseudofusus palatina* with both types of cirriped larval stages (10x)
38. *Ancilla glandiformis* with crab-made injure (2x)
39. *Ancilla glandiformis* with crab-made injures (2x)
40. *Potamides bidentatus margaritifer* with worm traces (4x)

Pl. VII

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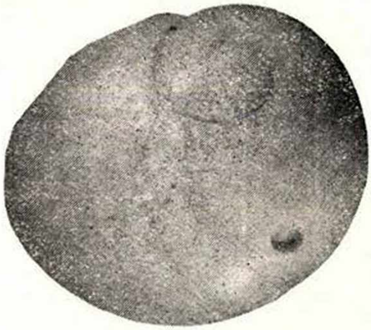

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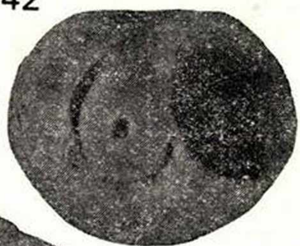

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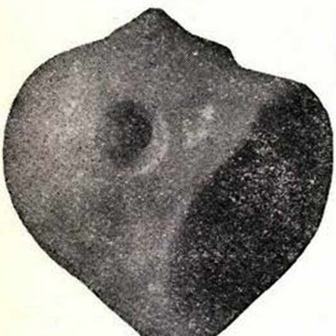

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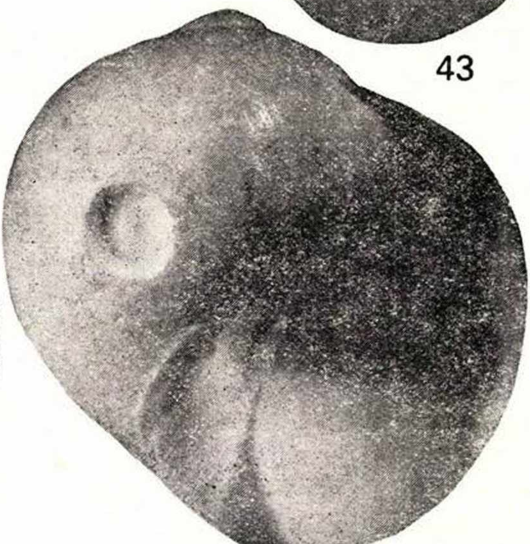

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PLATE VII.

41. *Melongena cornuta* with worm traces and boring bivalves (1x)
42. *Natica josephinia olla* with naticid boring (2.2x)
43. *Natica josephinia olla* with naticid borehole
44. *Natica millepunctata* with naticid boring (4.5x)
45. *Natica millepunctata* with naticid boring (5.3x)

Pl. VIII

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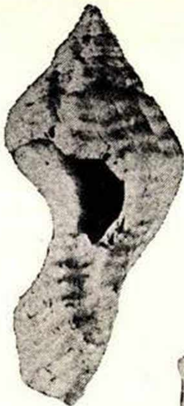

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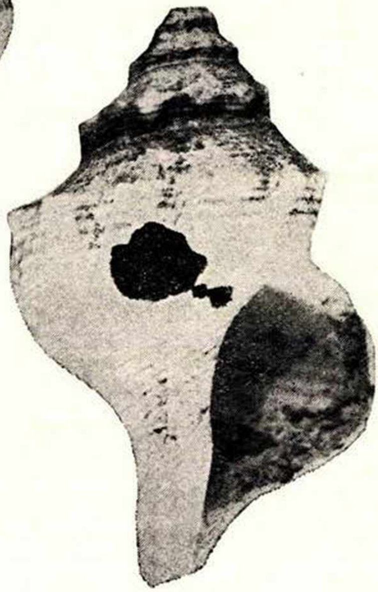

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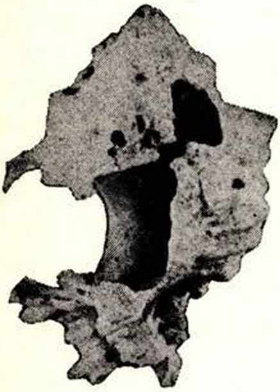

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PLATE VIII.

46. *Ocinebrina crassilabiata* with crab pinch (2.4x)
47. *Hadriania boeckhi* with crab pinch (2.4x)
48. *Euthriofusus burdigalensis* with crab pinch. (2.3x)
49. *Murex rudis syrticus* with crab pinches and boring bivalves. (1.5x)
50. *Murex rudis syrticus* with crab damages and the location of boring bivalves (1.5x)

Pl. IX

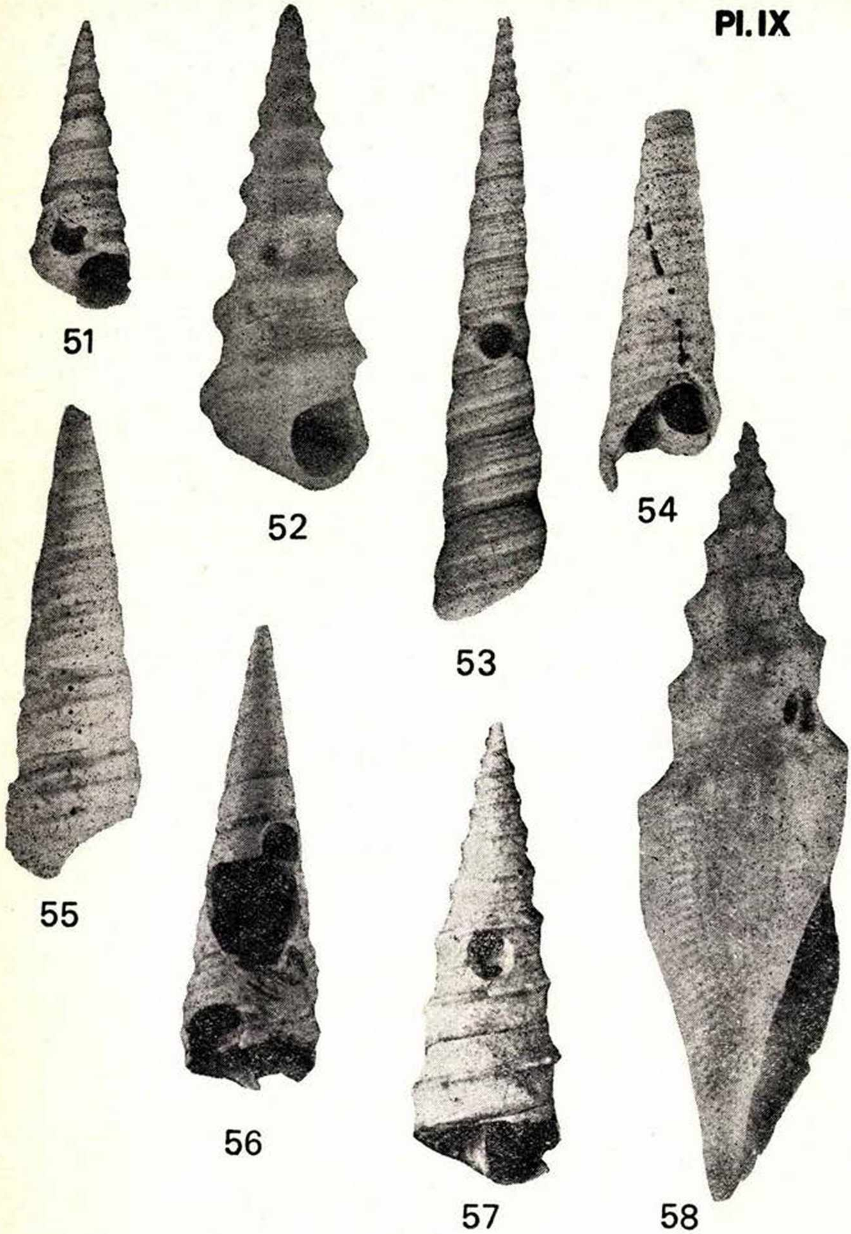
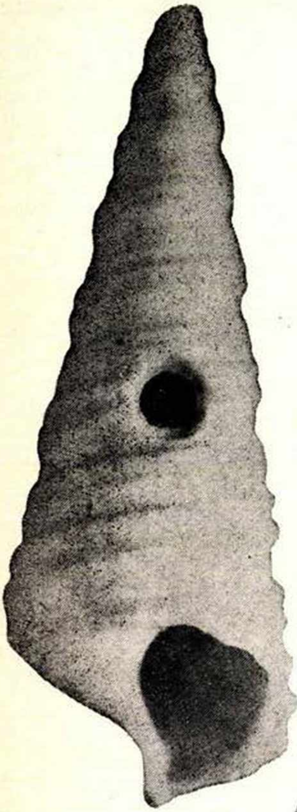


PLATE IX.

51. *Turritella aquitanica* with crab pinch (1.8x)
52. *Turritella aquitanica* with an unfinished boring of a naticid (3x)
53. *Turritella eryna partschi* with naticid borings (3.2?)
54. *Turritella turris badensis* with sponge pores (2.55)
55. *Turritella vermicularis* with sponge pores (3x)
56. *Turritella vermicularis* with naticid borings
57. *Turritella bicarinata subarchimedis* with naticid boring (3x)
58. *Genota ramosa elisae* with naticid boring (4x)

Pl. X



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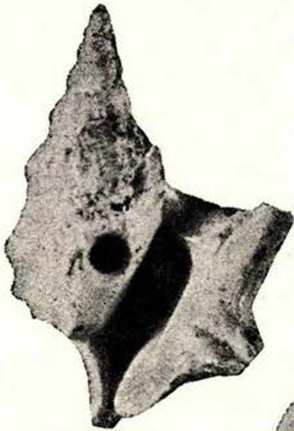

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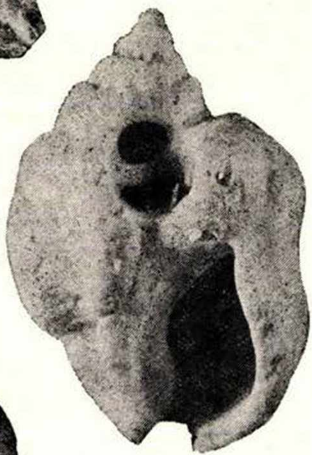

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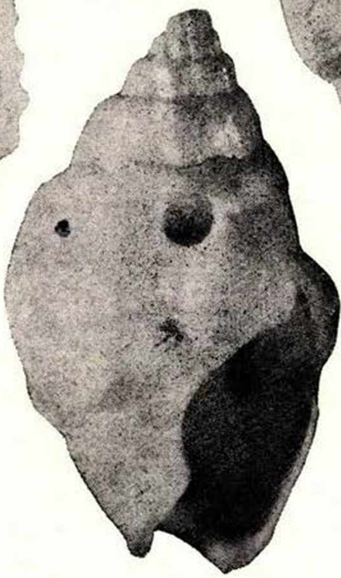

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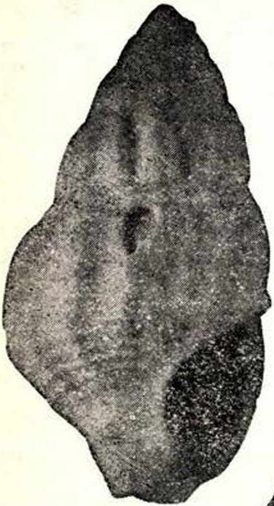
PLATE X.

59. *Protoma proto quadriplicata* with naticid boring (3.5x)
60. *Aporrhais pespelecani alatus* with naticid boring in the inner lip (4.6x)
61. *Nassa dujardini edlaueri* with naticid boring (5x)
62. *Nassa dujardini edlaueri* with naticid borings (5x)

Pl. XI



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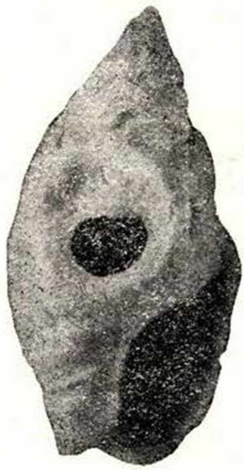

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PLATE XI.

63. *Nassa hungarica* with regeneration (6.5x)
64. *Dorsanum nodosocostatum* with traces of regeneration (5x)
65. *Dorsanum nodosocostatum* with naticid boring (5x)
66. *Dorsanum nodosocostatum* with naticids (6.5x)
67. *Terebra basteroti* with naticid borings (2.2%)

often attacked by the predators. The order within this major grouping was determined by the size, motility, shell thickness, ornamentation, and probably "taste" of the victim. For example 49 of 521 specimens of *Nassa dujardini edlaueri*, and 58 of 444 specimens of *Turritella aquitanica* were attacked by naticids. The case of it might have been the larger size of *Turritella*, thus yielding more food with the same effort; or the predator Nassas are more motile than the Turritellas living in the mud with their apex below the surface.

Plot of the victims of the muricids (Fig. 5) shows that though the several *Potamides* species are the same in habitat, size and shape, differing in their ornamentation only, the predators made important distinctions among them; possibly these were of different taste.

Table II indicates that the naticids and muricids attacked only some individuals of the too small *Theodoxus pictus*, and none of the too big *Potamides bidentatus perrugatus*.

A full picture on the diet of the predators can be drawn only if the traces on the bivalves will be studied, too. The main food of naticids and muricids are bivalves (Tatishvili et al., 1968). Our results support it: 308 naticid predators were compated with only 289 gastropod victims, while 81 muricids were compated with 362 victims.

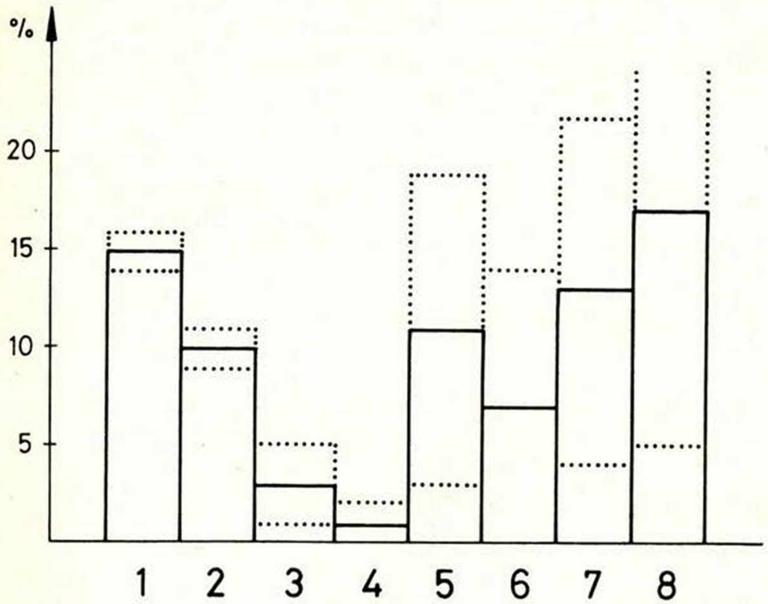

Fig. 5. Percentage of bored specimes of the species attacked by muricids (the species represented by more than 10 individuals are listed only). 1. *Potamides (Pirenella) gamlitzensis* 2. *Potamides (Pirenella) moravicus* 3. *Potamides (Pirenella) pictus* 4. *Potamides gamlitzensis theodiscus* 5. *Pusionella pseudofusus palatina* 6. *Cerithium rubiginosum pseudobliquistoma* 7 *Cerithium exdolium* 8. *Cerithium vulgatum europaeum*

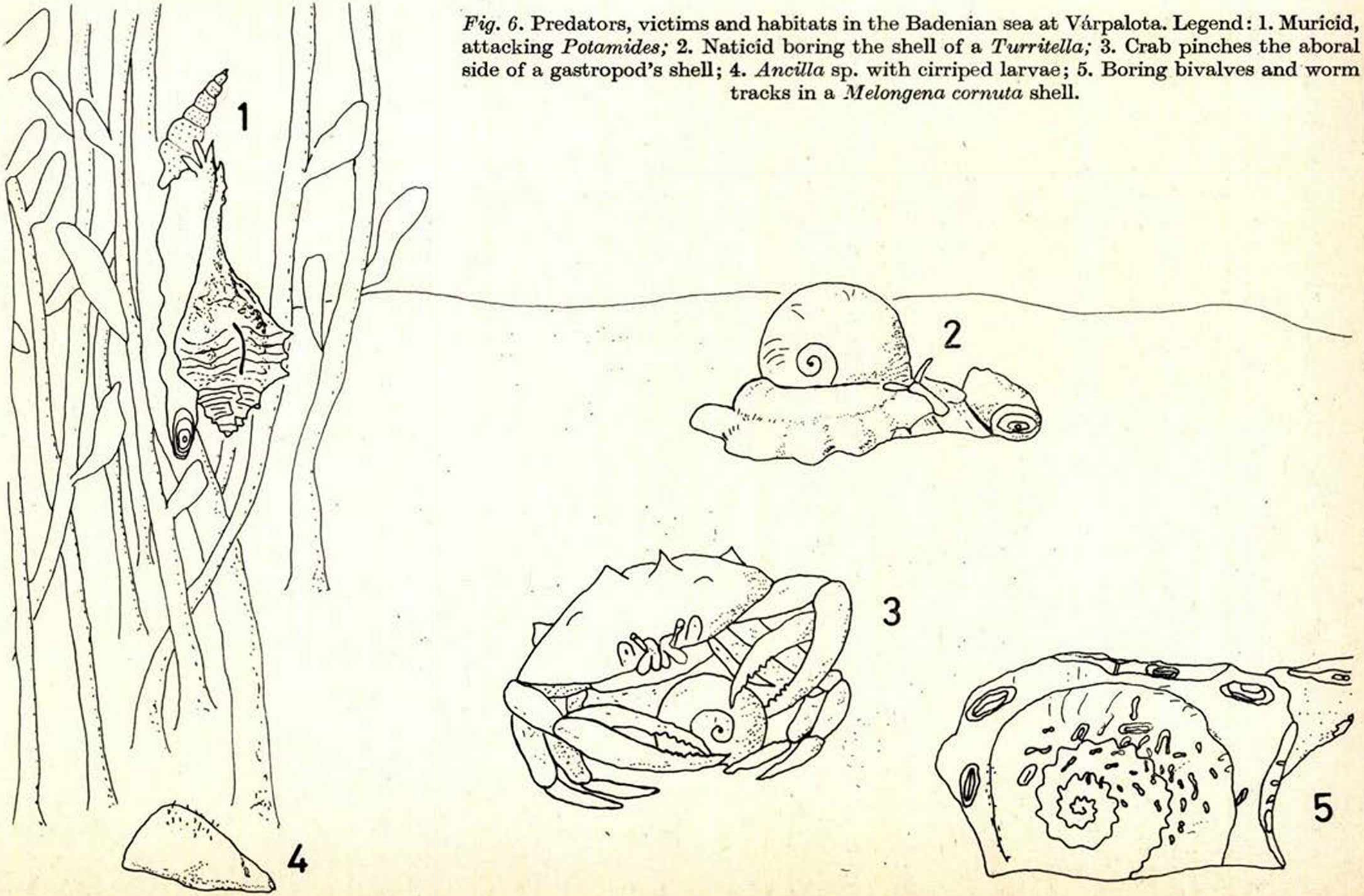

Fig. 6. Predators, victims and habitats in the Badenian sea at Várpalota. Legend: 1. Muricid, attacking *Potamides;* 2. Naticid boring the shell of a *Turritella;* 3. Crab pinches the aboral side of a gastropod's shell; 4. *Ancilla* sp. with cirriped larvae; 5. Boring bivalves and worm tracks in a *Melongena cornuta* shell.

Trace fossils made by different organisms usually occur on certain areas of the shell: traces of malacostracans are on the aboral side, traces of cirriped larvae are located in less exposed parts of the external side of the shells, and traces of boring bivalves occupy the regions with thick shell.

Trace fossils on gastropods indicate the major role of bioerosion in the preservation of shells.

The Badenian sea bottom is figured on Fig. 6. Habitats and feeding habits of fossilized animals and of animals which produced the trace fossils are figured in their natural environment.

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